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USING TAXONOMIC DATA TO ESTIMATE SPECIES RICHNESS IN GEOMETRIDAE

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ABSTRACT. A global database of described species was constructed for the Geometridae from the card index to genera and species housed in The Natural History Museum, London. Associated biogeographical data show that compared with existing estimates, marked differences exist in the number of described species in certain of the main biogeographical regions. The *actual* number of geometrid species depends on the number of species yet to be discovered or named and on the number of names of presently accepted species requiring synonymy. Evidence from recent revisionary work on selected Neotropical Geometridae based on both modern samples from Costa Rica as well as older museum material, and a qualitative assessment of taxonomic work on the family globally, suggests that the actual number of valid species is nothing like an order of magnitude greater than the number currently described.

Additional key words: biodiversity, systematics, biogeographical diversity, moths.

A large quantity of taxonomic data lies available but little used in those institutions housing collections and associated reference material. In the present study we have collated such information for Geometridae from card indices and other sources held in The Natural History Museum, London (NHM), an institute housing a large and well curated collection of this group organized on a world basis. From these data we provide a total for the number of *described* species globally and totals for each of the main biogeographical regions. The information indicates taxonomic effort on Geometridae, highlighting strengths and weaknesses in the taxonomy of a large and widely distributed group of terrestrial invertebrates.

The magnitude of *actual* number of species by biogeographical area also is considered by qualitative assessments of the level of taxonomic effort by region, and by using the results of recent sampling and revisionary studies on Costa Rican Geometridae to assess levels of taxonomic change.

The work forms part of a broader project, intended as a response to calls from the wider biological community, conservationists in particular, for systematists to find ways of making their information more accessible and more rapidly available (e.g., McNeely 1992, Wilson 1992, Janzen 1993).

Geometridae were chosen for this study for several reasons. First, they are one of the largest families of Lepidoptera and are distributed in all the main biogeographical regions. Second, much information has been gathered about them: the entire geometrid collection at the NHM is arranged and indexed taxonomically on a world basis, and contains much unpublished detail on synonymy and generic assignment. Third, recent taxonomic revisions have been undertaken for several subgroups. Over the past few years species-level taxonomy of several Neotropical genera has been undertaken by members of the Geometridae Research Group at the NHM. These studies made use not only of older material housed in museum collections but also modern samples, particularly those of the Instituto Nacional de Biodiversidad (INBio), Costa Rica. The results enabled us to gain some idea of the number of new species to be expected with access to specimens collected during a program of sampling in a biodiverse tropical country. Although the sample of genera studied was limited, it provided us with a guide to the *magnitude* of the number of new species expected with modern collecting.

METHODS

The Database

The foundation for this study is a computerized database, generated principally from the card index to the geometrid collections of the NHM. Names of putatively valid species, already described, were included in the database. The card index is complete, to within a small percentage, to 1985. Names of species from major sources published since then, up to October 1993 when the databasing finished, also were incorporated. As far as possible, the following information was recorded for each species of the six subfamilies (Archiearinae, Oenochrominae *sensu lato,* Ennominae, Geometrinae, Sterrhinae, and Larentiinae): author; date of description; type locality; and biogeographical area. Data were available for over 75% of species names for most variables, and in some cases for over 90%.

Numerous unpublished taxonomic changes, also incorporated in the database, were made to the collection and card index during the course of detailed curation by D. S. Fletcher and his associates over many years. The efforts of these curators added substantially to the pioneering work of L. B. Prout. These unpublished changes include the generic reassignment of many species and much species synonymy.

The biogeographical region for which the type locality was scored is that followed in the NHM collection and card index. These areas are Wallace's biogeographical regions with some subdivision. They are: Nearctic, Neotropical, Afrotropical, Madagascar, Western Palaearctic, Eastern Palaearctic, Indo-Pacific (including New Guinea, i.e., Irian Jaya/Papua New Guinea), Australasia, and New Zealand (see Gaston & Hudson *in press* for a map showing their distribution). The regions were accepted for their expediency rather than their biogeographical reality. Particularly controversial are: (i) the position of the dividing line between the Nearctic and the Neotropical regions; (ii) the position of the line dividing the Palaearctic from the Indo-Pacific region; (iii) the division between the Indo-Pacific region and Australasia—in particular the inclusion of New Guinea in the former rather than the latter; and (iv) the division between the Western and Eastern Palaearctic.

For the purposes of this work, species were taken to mean 'taxonomic' species. Although there is no agreement over the precise definition of a species for the Geometridae, or any other group of organisms, there is a general consensus among taxonomists as to what constitutes a geometrid species. While most geometrid species can be recognized on wing pattern, species-level decisions have been greatly refined by the study of the genitalia of these insects. The study of genitalia has affected species decisions in two ways. It has resulted in considerable synonymy of 'species' now considered to be just variations and, in contrast, it has led to the recognition of additional species previously unrecognized on the basis of wing shape or color. The study of genitalia has strongly influenced species taxonomy in Geometridae from around the time of the second world war, although A. J. T. Janse made extensive use of these structures in his work on the South African fauna earlier (Janse 1932, 1933–35).

The database took one person about nine months of full time work to complete.

RESULTS

Number of Described Species of Geometridae Globally and by Region compared with Estimates made by Heppner (1991)

Heppner (1991) tabulated the number of described species of Geometridae by biogeographical area and subfamily as part of a collation of described species for all lepidopteran families and subfamilies. Although the *total* number of species for the Geometridae given by Heppner differs by less than 1.5% from our own, the differences between the two sets of figures in some of the biogeographical regions are very great (Table 1). Since the biogeographical areas used by Heppner (1991) differ in some instances from those used in our database, we made our figures comparable by adding and subtracting species numbers where necessary. The source of our regional figures in Table 1 is the database (see Methods), adjusted, for some areas, by those additional sources indicated below.

Nearctic. Our figures (Table 1) are those of the lepidopteran checklist by Hodges et al. (1983). There have been some additions and synonymys since that time, but these are not extensive.

Neotropical. The database includes results of some revisionary work

TABLE 1. Numbers of described species of Geometridae by biogeographical region.

	NEA[1]		NEO		PAL		AFR[2]		ORI		AUS[3]		Total	
E	750	769	3318	3948	1361	1644	1556	863	1846	1240	879	520	9710	8984
L	466	471	1668	2137	1398	1511	464	501	1042	803	711	300	5749	5723
S	95	96	902	906	526	681	480	380	543	564	217	220	2763	2847
G	73	76	454	651	220	326	561	300	584	431	404	475	2296	2259
O	3	3	87	310	34	75	45	100	136	227	305	350	610	1065
A	2	2	4	4	6	6	0	0	0	0	4	0	16	12
	1398	1417	6433	7956	3545	4243	3106	2144	4151	3265	2520	1865	21,144	20,890

Our figures are not underlined; figures underlined are from Heppner (1991). To equate biogeographical areas used in our database with those of Heppner, we summed species numbers in the following regions: Western and Eastern Palaearctic (combined as Palaearctic by Heppner); Afrotropical and Madagascar (combined as Afrotropical by Heppner); Australia, New Zealand and Oceania (including Irian Jaya/Papua New Guinea) (combined into Australasia by Heppner).

E, Ennominae; L, Larentiinae; S, Sterrhinae; G, Geometrinae; O, Oenochrominae; A, Archiearinae.

[1] Our figures are taken from the *Check List of the Lepidoptera of America North of Mexico* (Hodges et al. 1983).

[2] Includes Madagascar.

[3] Our figures are based on the estimates of described species by Common (1990) for Australia, from the species catalogued by Dugdale (1988) for New Zealand and, for Oceania, from a summation of the type localities with additions of those species listed as endemics from Hawaii in Nishida (1992).

in press. These additions, however, will not have increased significantly the number of names in this region.

Palaearctic. Obtaining figures for numbers of described species in the Western and Eastern Palaearctic is complicated by the existence of various country lists for Europe: figures based on such lists would result in duplication of many species names. Our figures therefore are based strictly on the database of type localities. Many of those localities that we failed to identify in the time available are likely to fall in the Palaearctic, and the position of the border between the Palaearctic and the Indo-Pacific regions is such that some uncertainties exist over the regional designation of some species. We have resolved these problems as far as possible, but they are more likely to bias our figures on the low than on the high side.

Afrotropical (Ethiopian). The number of geometrid species in the database with a type locality in Madagascar is 649, while in the checklist of Madagascan Lepidoptera compiled by Viette (1990) the number is 665. These two figures correspond well, particularly as in the checklist the total would be expected to be somewhat higher by including species occurring both in Madagascar and Africa. The number of geometrid species for Southern Africa (including Namibia, Botswana, Zimbabwe, Mozambique south of the Zambesi, South Africa and the constellation of countries within South Africa) listed by Vári and Kroon (1986) is 914. Thus, total geometrid species for Southern Africa (Vári & Kroon's figure) plus Madagascar (the figure from our database) is 1563, leaving a figure of 1543 further species for the rest of the Afrotropics. By no means does this latter figure seem unreasonable for described species in this area.

Numbers of geometrid species by subfamily estimated by Herbulot (1992) for the Afrotropical region are as follows: Ennominae, 1608; Larentiinae, 467; Sterrhinae, 469; Geometrinae, 572; Oenochrominae, 52. These figures are broadly similar to ours (see Table 1). While our estimate of the total number of species differs by merely 2% from that of Herbulot, it is 45% higher than that of Heppner.

Oriental. Our figures were produced by subtracting from the number of Indo-Pacific records in the database the number of species listed from the Pacific Islands east of, and including, New Guinea.

Australasia. Our figures for the number of described species in Australia are those of Common (1990); those for New Zealand were derived from the checklist by Dugdale (1988). For the Pacific Ocean islands we summed the number of type localities recorded in the database.

The Magnitude of Actual Numbers of Geometrid Species

Understanding the true number of geometrid species depends on the number of species already described, the number of species undescribed (whether represented in collections or not) plus species needing to be revived from synonymy, and the number of species names requiring synonymy. Accumulation curves of geometrid species numbers by decade (Gaston, Scoble & Crook in press) show that the rate at which species were described rose rapidly from around 1850 and, for several regions, fell sharply around the time of the second world war. There are several possible reasons for the fall in species description rates; a reduction in the number of new species to be described is only one.

Nearctic. Taxonomic knowledge for Geometridae in the Nearctic region is fair to good. The area has benefited from a comprehensive checklist of Lepidoptera (Hodges et al. 1983), in which many revisionary changes to the taxonomy have been incorporated. Nine authors, from a total of over 75, are collectively responsible for the description of around 70% of geometrid species from this region. They are: W. Barnes, S. E. Cassino, J. A. Grossbeck, A. Guenée, G. D. Hulst, J. H. McDunnough, A. S. Packard, F. H. Rindge, and F. Walker. Continued collecting, and study of unworked material stored in institutions, will undoubtedly reveal undescribed species, and further revisionary work will almost certainly identify further synonyms. Nevertheless, fieldwork over a long period by many individuals suggests that the number of species yet to be collected is unlikely to be high.

Neotropical. This region has the greatest number of described geometrid species, although the rate of description declined in the second decade of the century. It is likely also to have the greatest actual number of species.

Taxonomic knowledge of Neotropical Geometridae is fragmentary with modern revisions available for relatively few of the many genera. Eight authors, from a total of around 70, are collectively responsible for the description of over 75% of all geometrid species from the region. They are: P. Dognin, H. Druce, A. Guenée, L. B. Prout, F. H. Rindge, W. Schaus, F. Walker, and W. Warren. Of these, only F. H. Rindge is responsible for modern revisionary work (almost exclusively on selected genera of Ennominae) involving the study of genitalia. To gain a useful estimate of actual geometrid diversity in the Neotropics will require more even sampling over the region and more, and better planned, revisionary work incorporating material from the numerous and scattered collections of Neotropical geometrids.

Palaearctic. In the database, this region is subdivided into Western and Eastern Palaearctic. Assessing the true number of species in the Western Palaearctic is surprisingly difficult given such considerable taxonomic effort, including collecting, over a long period. The rate of description of new species shows no sign of decline in the subregion.

The extensive review of Palaearctic Geometridae by Prout (1912–

16, 1934–39), which did not involve morphological study of the genitalia, provides a useful taxonomic base. Revisionary work since then has been patchy. Few works cover taxa across the region and there are many subregional (often country) treatments. While much valuable information exists for Palaearctic Geometridae, coordination of effort is likely to result in numerous taxonomic changes at the level of species (and genus). The need for coordination and revision is acute in the Western Palaearctic subregion because the taxonomic effort, in terms of species descriptions, is more evenly spread, involving substantially more individual workers than any full biogeographical region.

The species taxonomy of the Eastern Palaearctic is more poorly documented; sampling has been less intense for much of the subregion. Our understanding of the Geometridae of Palaearctic China is relatively poor, while in Japan it is good with numerous revisions particularly by H. Inoue. Nine individuals (A.G. Butler, H. Inoue, J. H. Leech, C. Oberthür, L. B. Prout, O. Staudinger, A. Vojnits, W. Warren, and E. Wehrli) are responsible collectively for the description of around 70% of the named species of the Eastern Palaearctic.

Afrotropical. Our knowledge of Afrotropical Geometridae is uneven across the continent. The work of Janse (1932, 1933–35), which included morphological study of the genitalia, forms an invaluable basis for the Geometridae of South Africa, and has been influential in the taxonomy of the group for the rest of Africa. A recent checklist of Lepidoptera of the subcontinent (Vári & Kroon 1986) incorporates taxonomic changes since the time of Janse's revisionary studies. North of South Africa the geometrids are less well studied although a number of comprehensive revisions have been published. Just four individuals (D. S. Fletcher, C. Herbulot, L. B. Prout, and W. Warren) are collectively responsible for describing around 75% of the species. In Madagascar, treated separately from the rest of the Afrotropical region in the database, the number of names of Geometridae is likely to increase with further collecting and revisionary treatments. Just three authors (C. Herbulot, L. B. Prout, and P. Viette) are responsible for the description of around 80% of the species.

The rate of description of species shows little sign of declining either in Africa or Madagascar, but revisionary work will undoubtedly lead to much synonymy besides additional new species.

Indo-Pacific. Taxonomic knowledge of Geometridae from the Indo-Pacific region ranges from poor to fair across taxa and subregions. Most of the 5123 described species from the area were named before the level of revisionary work was advanced by the study of genitalia. However, revisionary study is particularly good for the Ennominae of Borneo (Holloway 1994). Given the intensity of sampling in Borneo, the number of geometrid species yet to be collected is unlikely to exceed 10% of the number recognized currently (J. D. Holloway pers. comm.). Other areas that have benefited from modern revision or review of geometrid moths are Norfolk Island (Holloway 1977), New Caledonia (Holloway 1979), Fiji (Robinson 1975), Hawaii (Zimmerman 1958, Nishida 1992), and Nepal (Yazaki 1992, 1993, Sato 1993). Seven individuals are responsible for describing around 75% of the species. They are: G. F. Hampson, H. Inoue, F. Moore, L. B. Prout, C. Swinhoe, F. Walker, and W. Warren.

Among the Pacific islands, the number of new species from New Guinea, especially, is likely to rise substantially given the high level of endemicity of its fauna, our relative ignorance of its geometrids, and the number of complexes of closely related, externally similar, species it appears to support.

Australia. The actual number of geometrid species in Australia was estimated as 2310 (Nielsen & Common 1991), a figure based on considerable taxonomic effort in the preparation of a forthcoming checklist of Australian Lepidoptera (Nielsen et al. in prep.). This figure is almost double the number of species described. The existence of many undescribed species is explained by the description of few geometrid species since 1947, a date representing the end of studies by A.J. Turner, and extensive collecting from 1960 onwards (E. D. Edwards pers. comm.). Current collecting activity is resulting in the discovery of very few species that are undescribed or unrepresented in collections. Thus the actual number of geometrid species in Australia is unlikely to more than double the number described.

Around 75% of Australian geometrid species have been described by four individuals: O. B. Lower, E. Meyrick, A. J. Turner, and F. Walker.

New Zealand. The accumulation curve for description of geometrid species reaches an asymptote around the decade commencing 1940 (Gaston, Scoble & Crook in press). It seems unlikely that the number of species will increase greatly, and certainly not by an order of magnitude (J. S. Dugdale pers. comm.).

Around 75% of New Zealand geometrid species were described by four individuals: G.V. Hudson, E. Meyrick, A. Philpott, and F. Walker.

Using Recent Samples and Taxonomic Revision to Estimate Actual Species Numbers

Museum collections of geometrids (and other organisms) are neither comprehensive nor do they represent a random sample of species. The comprehensiveness of taxonomic revisions based on them are, therefore, limited correspondingly. Revisionary works most likely to give a best

TABLE 2. Changes in selected genera of Neotropical Geometridae after recent taxonomic revision.

	Oos	*Nem*	*Lis*	*Cha*	*Thy*	*Per*	*Phr*	*Pit*	Total
No. of species after revision	72	99	42	14	12	24	13	2	278
No. of new species[1]	3	29	3	0	4	15	4	0	58
No. of names synonymized[2]	37	9	11	3	2	1	20	5	88
% new species	4	29	12	0	33	62	31	0	21
% new synonymy	50	9	26	24	16	4	154	250	32

Abbreviations of genera, and sources from which the data were derived. *Oos*, *Oospila* (Geometrinae) (Cook & Scoble in press); *Nem*, *Nemoria* (Geometrinae) (Pitkin 1993); *Lis*, *Lissochlora* (Geometrinae) (Pitkin 1993); *Cha*, *Chavariella* (Geometrinae) (Pitkin 1993); *Thy*, *Thysanopyga* (Ennominae) (Krüger & Scoble 1992); *Per*, *Perissopteryx* (Ennominae) (Krüger & Scoble 1992); *Phr*, *Phrygionis* (Ennominae) (Scoble 1994); *Pit*, *Pityeja* (Ennominae) (Scoble 1994). The figures were derived from results in revisions using material from the NHM and INBio in all genera listed. Material from several North American museums was incorporated into revisions for all genera excepting *Thysanopyga* and *Perissopteryx*.

[1] Includes revived species (names removed from synonymy).

[2] Refers to names synonymized in the works listed, not necessarily the total number of synonyms. Includes changes of status of species to subspecies.

estimate of numbers of new species are those involving a well organized sampling program.

Taxonomic study of selected neotropical genera incorporating material from recent collecting in Costa Rica shows that for, admittedly, a non-random sample of taxa, the increase in numbers of species can be strongly reduced by the number of species synonymized (Table 2).

DISCUSSION

Described Species

We are unclear as to the sources of many of the species numbers given by Heppner (1991) (Table 1). They were provided for the Nearctic region, for Australia, and for New Zealand but there is no convincing explanation as to how the other figures were derived. Robbins already has suggested that the figures in Heppner's tables for butterflies (taxonomically the best known Lepidoptera) should not be used for diversity studies unless the apparent high bias is documented. We urge similar caution in the use of Heppner's figures for diversity studies in Geometridae until it can be convincingly demonstrated that they are more soundly based than our own.

The validity of the species accepted in the database depends on the accuracy of geometrid taxonomy. The number of synonyms in Table 2 suggests that many of the species we accept as valid today may be synonymized with future revisionary work.

Actual Numbers of Species

Accounting for synonymy is of great relevance in attempting to estimate *actual* species numbers (Gaston & Mound 1993). Table 2 shows how synonymy may be much underestimated in species richness assessment. Even with the many unpublished synonymies recorded in the database, detailed revisionary work identifies many more. In a study of ennomine geometrids of Borneo, Holloway (1994) recognized 429 species, 83 of which were new, and 13 of which were revived from synonymy. Fifty-six new synonymies were made. Unlike the situation in Table 2 for certain Neotropical genera, in Holloway's study synonymy was only 13% of the total species finally recognized as valid. Nevertheless, synonymy is evidently of critical importance in estimating species numbers, yet it is widely ignored in the literature on biodiversity—the description of new species being given overwhelming, and uncritical, emphasis.

From Table 2 it is clear that access to extensive modern collections from the tropics does not necessarily result in the description of proportionally large numbers of new geometrid species. When synonymy is accounted for, the overall figure for geometrid species will rise even less. Although most geometrid genera are relatively cryptic, and thus prone to under-description, there are no signs that the total number of species is set to rise by anything remotely like an order of magnitude, even in the Neotropics—the most species-rich of the biogeographical areas.

We emphasize that the figures in Table 2 provide only an indication that species richness is not as great as we are sometimes led to believe. Limitations to sampling in other parts of the Neotropics provide us with little idea as to the true extent of geometrid species richness outside Costa Rica. Nevertheless we find the figures suggestive and hope that a similar exercise will be undertaken for other Lepidoptera and that the work will be expanded to incorporate modern samples from Neotropical sites outside Costa Rica.

Care also should be taken in extrapolating from the results in Table 2 for, as lepidopterists are well aware, brightly colored or strikingly patterned Lepidoptera are far more likely to suffer from variants being described as species. The dramatic synonymy recorded in Table 2 for the genera *Phrygionis* and *Pityeja* is undoubtedly so explained and, in any case, *Pityeja* is a very small genus. In contrast, more cryptic Lepidoptera tend to be underdescribed—as in the ennomine genus *Perissopteryx* in which many new species were described. Table 2, however, includes a spread of genera from those with species often difficult to distinguish on wing pattern (*Thysanopyga*, *Perissopteryx*, *Nemoria*), through *Oospila*, a genus with species that usually can be effectively distinguished on wing pattern, to genera exhibiting marked variation within species (*Phrygionis* and *Pityeja*). Although the sample of geometrid genera is representative neither of the Neotropics nor of geometrid genera globally, nothing in the results suggests that there exists for this family the massive number of undescribed species estimated by Erwin (1982) to apply to insects generally. However, because collecting falls well short of comprehensive coverage (particularly in diverse regions such as South America), it is impossible to be precise about the actual global number of geometrid species.

A message from this study is that taxonomic data provide a useful source of information about species richness (e.g., Gaston 1991), a theme we are developing further for the Geometridae in particular. A proviso is that such data require careful and critical assessment. Unevenness of sampling is a particular problem, and older taxonomic works require revision to provide a balanced view of species numbers and species identity.

The value of taxonomic revisionary work in the modern biodiversity arena, as opposed to just the description of new species, is immense and not well appreciated (e.g., Albert 1993) by biologists generally. Although, and not surprisingly, its value is far better understood by taxonomists, there are few signs of the coordination and planning necessary to achieve taxonomic coverage sufficiently comprehensive to make a profound impact on our understanding of biodiversity (Mound & Gaston 1993). Furthermore, the usefulness of inventories and 'quick and dirty' lists as a base on which general biological data can be associated depends strongly on the quality of our taxonomic knowledge.

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